

Fluid-Dynamic Drag of Limpet Shells

by

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Abstract. This study examines the hydrodynamic significance of limpet shell morphology. An elongate shell and eccentric apex contribute to a streamlined form. The degree of apex eccentricity cannot, however, be explained solely as a consequence of drag reduction. Limpet shells are generally better streamlined than round protrusions. That there has been selective pressure for drag-reducing features is supported by the finding that those limpet species living in heavily wave-stressed environments experience a lower relative drag than their unstressed counterparts. Finally, relative projection of a shell into the boundary layer can strongly influence the dependence of drag upon free-stream velocity, a condition that may be of importance in the settlement and survival of those small, particularly larval forms in the intertidal zone.

INTRODUCTION

LIFE IN THE INTERTIDAL zone is characterized by exposure to significant forces of fluid drag and wave impact. The shell morphology of intertidal gastropods often incorporates drag-reducing features. It has been demonstrated that streamlining, as indicated by an anteriorly shifted apex, a large aperture relative to height, and a fineness ratio (length to width) significantly above unity, is generally characteristic for wave-exposed littorines (STRUHSAKER, 1968; HELLER, 1976), muricids (KITCHING & LOCKWOOD, 1974), and limpets (GRAHAM & FRETTER, 1947; DURRANT, 1975; LEWIS & BOWMAN, 1975; WARBURTON, 1976). Limpets are common intertidal gastropods whose depressed shells and noteworthy powers of tenacity seem particularly well-suited to conditions of heavy wave exposure. Surprisingly, only one attempt has been made to measure experimentally the drag forces on limpet shells. BRANCH & MARSH (1978) determined drag forces and coefficients of drag (C_D) for six species of *Patella* from South Africa. Their experimental design, however, lacked verisimilitude in that limpet shells were apparently placed in the free stream of flow, rather than as in the natural setting adjacent to a surface with a clearly defined boundary layer of fluid. Moreover, their data indicate a nearly inverse relationship between C_D and the Reynolds number ($C_D \propto Re^{-0.95}$). The Reynolds number for a particular situation of flow is defined as $Re = lU/\nu$, where l is some characteristic length of the object, U the

fluid velocity, and ν the kinematic viscosity of the fluid. As noted by VOGEL (1981), the only objects known that exhibit such an inverse relationship between C_D and Re are those that can reshape themselves with increasing velocities, such as trees. In this particular range of Reynolds number (10^3 to 10^5) $C_D \propto Re^0$, while for long flat plates parallel to flow, $C_D \propto Re^{-0.5}$ (HOERNER, 1965). The generally conical or ellipsoidal limpet shell in free-stream flow might well be expected to display a relationship more similar to that of a bluff body than that of a flat plate. The present study examines drag forces on limpet shells near a substratum. Drag is related to various morphological parameters, and the peculiar variation of C_D with Re for limpets within a relatively large boundary layer is noted.

MATERIALS AND METHODS

Drag forces on shells were measured in a continuously circulating flow tank (VOGEL & LABARBERA, 1978). Velocity was calibrated visually with ink at low velocities, and for higher velocities was derived from drag measurements of simple geometrical objects with known drag coefficients. Maximum tank velocity was 0.45 m/sec. In the working section of the tank (height 8.8 cm, width 10.4 cm), a thin plexiglas plate (20.3 by 8.7 by 0.2 cm, with a bevelled anterior edge) was fixed, parallel to flow, 4 cm below the water's surface (Figure 1). Limpet shells were filled with hard wax, and were positioned upside-down, 0.85 mm from the lower surface of the plexiglas plate. The center of each shell was 11 cm from the leading edge of the plate. A metal rod (1.5 mm in diameter) ran upwards from the center of the wax mass, through an open-

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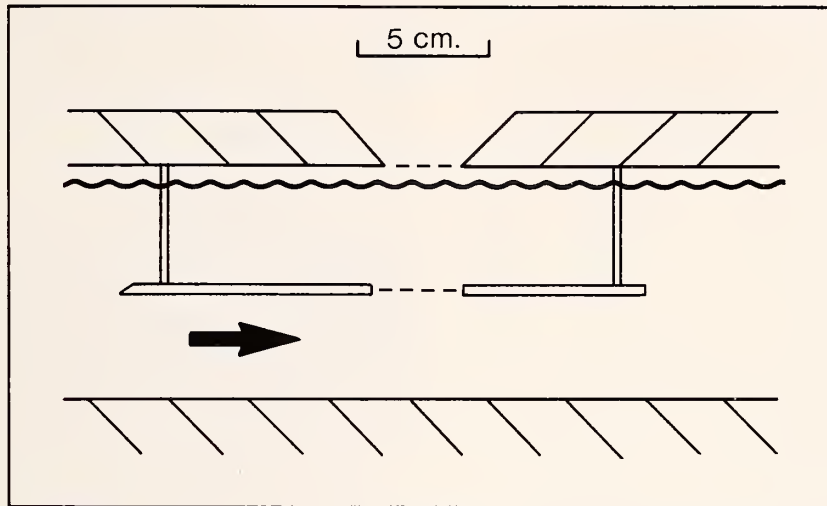


Figure 1

Lateral view of the working section of the flow tank.

ing in the plate (3 by 0.43 cm), to a thin metal strip (0.03 cm shim stock), in turn fixed firmly to the flow tank platform (Figure 2). A pair of strain gauges, attached to either side of the metal strip, were used as elements of a Wheatstone bridge, the output of which was amplified and displayed on a digital voltmeter. The voltage drop across the Wheatstone bridge was thus proportional to the drag force acting on the shell; the apparatus was calibrated by hanging weights from the end of the attachment rod, with the entire system held vertically. Reorientation of the shell with increased fluid velocity was observed to be minimal. For each shell, drag at a particular velocity was measured three times in each of three orientations: anterior end upstream, posterior end upstream, and shell lateral to flow. Drag measurements, with allowance taken for drag of the attachment rod, are estimated to be accurate to within 10%, and repeatable to within 5%.

The major and minor diameters, height from apex to base, and distances from the apex to the anterior and posterior shell margins were measured for 28 limpet shells with vernier calipers to within 0.05 mm. Perimeter measurements were taken from impressions in clay. The amount of water displaced by the shell and wax mass was taken as a measure of shell volume. Table 1 gives these data, along with geographical and ecological information for each limpet species. Also presented in Table 1 are the ratio X of the anterior to posterior distances from edge to apex (a measure of apex eccentricity), the fineness ratio R_F (major diameter/minor diameter, one possible measure of pressure-drag streamlining), and the relative shell height h_R , the ratio of the shell height to the geometrical mean of the major and minor diameters.

The drag of an object is related to the fluid velocity by the formula: $D = \frac{1}{2}C_D\rho SU^2$, where D is the drag, ρ the

fluid density, S a reference area of the object, U the fluid velocity, and C_D the aforementioned coefficient of drag, which for a given object and orientation is normally determined empirically. In practice, drag data are often reduced to a plot of C_D versus Re , with some reference cross-sectional or projected area taken for S . However, for a given object in a given medium, $C_D \propto D/U^2$ and $Re \propto U$. A plot of D/U^2 versus U will thus yield the same power dependence of C_D upon Re , the function being of the form $y = ax^b$. This latter approach is attractive in that any assumptions concerning the dimensions of often highly irregular biological objects are avoided. Volume to the

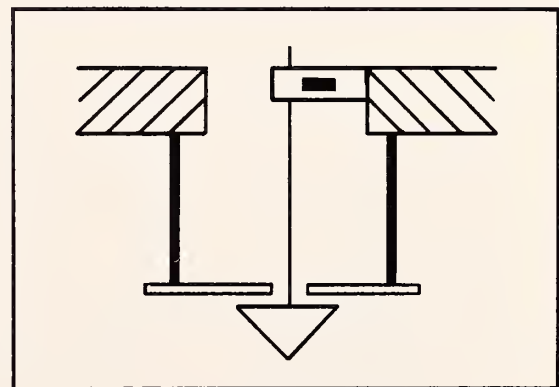


Figure 2

Details of the force transducer used in the drag measurements. Attached to one side of the shim stock is a strain gauge, given in black. The other strain gauge is hidden from view. Water flow is perpendicular to the plane of the diagram.

Table 1

Species identification, locale, habitat type, and morphological data for 28 limpet shells.

Shell no.	Species and locale	Habitat type
1	<i>Scurria scurra</i> (Lesson, 1830) Montemar, Chile	kelp stipes
2	<i>Scurria scurra</i> (Lesson, 1830) Montemar, Chile	
3	<i>Scurria scurra</i> (Lesson, 1830) Montemar, Chile	
4	<i>Patelloida saccharina</i> L. (1758) Ngeyanges, Palau	sheltered
5	<i>Patelloida saccharina</i> L. (1758) Ngeyanges, Palau	
6	<i>Patelloida saccharina</i> L. (1758) Ngeyanges, Palau	
7	<i>Patella flexuosa</i> (Quoy and Geimard, 1834) Salafai, Pagan	low intertidal, very heavily exposed
8	<i>Patella flexuosa</i> (Quoy and Geimard, 1834) Salafai, Pagan	
9	<i>Notoacmea inessa</i> (Hinds, 1842) Madison Port, Carmel, California	kelp stipes
10	<i>Notoacmea inessa</i> (Hinds, 1842) Madison Port, Carmel, California	
11	<i>Notoacmea inessa</i> (Hinds, 1842) Madison Port, Carmel, California	
12	<i>Collisella digitalis</i> (Rathke, 1833) Point Pinos, California	high intertidal and splash zones
13	<i>Collisella digitalis</i> (Rathke, 1833) Point Pinos, California	
14	<i>Siphonaria javanica</i> (Blainville, 1827) Rendrag, Palau	sheltered
15	<i>Siphonaria javanica</i> (Blainville, 1827) Rendrag, Palau	
16	<i>Siphonaria laciniosa</i> L. (1758) Rendrag, Palau	sheltered
17	<i>Siphonaria laciniosa</i> L. (1758) Rendrag, Palau	
18	<i>Fissurella nimbose</i> L. (1758) Rockoy, Guadeloupe	highly exposed, sand scour
19	<i>Fissurella nimbose</i> L. (1758) Rockoy, Guadeloupe	
20	<i>Fissurella nimbose</i> L. (1758) Rockoy, Guadeloupe	
21	<i>Fissurella nodosa</i> (Born, 1780) Fort Point, Jamaica	heavy exposure
22	<i>Fissurella nodosa</i> (Born, 1780) Fort Point, Jamaica	
23	<i>Nacella</i> sp. Tierra del Fuego	intertidal
24	<i>Nacella</i> sp. Tierra del Fuego	
25	<i>Nacella</i> sp. Tierra del Fuego	
26	<i>Patella vulgata</i> L. (1758) Cove, Scotland	moderate exposure

Table 1 (Continued)

Shell no.	Species and locale	Habitat type
27	<i>Patella vulgata</i> L. (1758) Cove, Scotland	
28	<i>Patella vulgata</i> L. (1758) Cove, Scotland	

The shell length l , width w , height h , volume V , perimeter p , fineness ratio R_F , eccentricity X , and the relative shell height h_R for 28 limpet shells. All lengths are given in millimeters, shell volume in milliliters.

Shell	l	w	h	V	p	R_F	X	h_R
1	27.2	23.5	18.1	4.1	79.7	1.15	0.98	0.72
2	21.7	19.4	11.5	2.0	65.0	1.12	0.83	0.56
3	17.5	15.4	8.4	1.0	52.5	1.14	0.85	0.51
4	23.2	19.4	11.5	1.3	70.1	1.19	0.89	0.42
5	21.3	18.5	7.2	1.1	66.1	1.15	0.83	0.36
6	17.5	13.5	5.4	0.4	48.3	1.30	0.89	0.35
7	41.5	29.6	9.2	3.3	118.9	1.40	0.73	0.26
8	34.5	26.5	6.5	2.9	97.9	1.30	0.71	0.22
9	16.2	10.2	9.5	0.9	42.5	1.59	0.82	0.74
10	15.5	9.4	8.5	0.5	40.0	1.64	0.79	0.70
11	14.4	9.7	8.0	0.3	39.1	1.49	0.71	0.67
12	20.4	16.6	8.6	1.8	57.3	1.23	0.46	0.47
13	21.0	21.0	7.8	1.1	74.8	1.00	0.38	0.37
14	22.6	19.2	11.6	1.2	65.8	1.17	0.94	0.56
15	21.6	15.1	9.2	0.9	55.8	1.43	0.82	0.51
16	25.2	22.5	6.7	1.0	75.4	1.12	0.90	0.28
17	21.6	19.6	6.5	0.9	66.9	1.10	0.88	0.31
18	36.2	24.1	12.3	3.9	94.9	1.50	0.79	0.42
19	27.6	19.5	8.3	1.7	72.8	1.41	0.80	0.36
20	17.4	10.3	6.3	0.6	45.8	1.68	0.83	0.47
21	32.9	21.4	17.8	4.8	90.2	1.54	0.96	0.67
22	21.0	18.3	12.8	2.6	71.4	1.15	0.92	0.65
23	48.2	40.0	24.7	24.0	137.8	1.20	0.80	0.56
24	32.0	25.5	20.7	7.5	90.5	1.25	0.90	0.73
25	61.4	42.4	12.3	22.0	164.8	1.45	0.55	0.24
26	41.8	34.6	17.4	10.0	121.9	1.20	0.85	0.46
27	35.0	29.2	13.3	4.9	102.5	1.21	0.83	0.42
28	29.7	24.7	13.1	4.0	84.8	1.21	0.73	0.48

power $\frac{2}{3}$ could well be the most biologically relevant reference area (VOGEL, 1981), but for craspedophilic organisms living in significant boundary layers it may not adequately reflect the relative importance of protrusion of the organism above the substrate. In the following analysis, the dependence of C_D upon Re will be determined from the equation $D/U^2 = aU^b$, but, for purposes of comparison with existing data, drag coefficients calculated on the basis of frontal (cross-sectional) area will also be presented.

RESULTS

A typical plot of drag versus velocity for shells in anterior, posterior, and transverse orientations is given in Figure 3.

After a logarithmic transformation of the quantities D/U^2 and U , linear regression ($\ln y = \ln a + b \ln x$) was used to determine a and b in the equation $D/U^2 = aU^b$. Correlation coefficients for this regression ranged from 0.91 to 0.99. From the two constants a and b , a "standard" drag for a particular orientation was calculated at a reference velocity of 0.3 m/sec from the formula $D = a(0.3)^{b+2}$. A mean drag, \bar{D} , was calculated for each shell from the formula $\bar{D} = (D_A + D_P + 2D_T)/4$, where D_A is the anterior drag, D_P the posterior drag, and D_T the transverse drag. The mean drag thus approximates from the experimental data the drag for a random orientation. Transverse drag was in all cases calculated only for the left side (with respect to the anterior-posterior) axis of the shell; limpets are generally, with the exception of the siphonariids, bilaterally symmetric, and for the sample of shells studied (excluding *Siphonaria laciniosa* and *S. javanica*) there was no significant difference in the shortest distance from the apex to the right and to the left side of the shell margin (χ^2 test, $P < 0.01$). From the anterior drag, a drag coefficient was calculated from the formula: $C_D = 2D/(\rho S U^2)$, where D and ρ are as previously given, U equals 0.3 m/sec, and S is the cross-sectional area normal to flow. Finally, considering each of the three orientations equally, a mean \bar{b} of the power b was calculated for each shell. Table 2 lists for each limpet shell D_A , D_P , D_T , \bar{D} , C_D , and \bar{b} .

Anterior drag was in most cases only slightly less than posterior drag. No correlation between the apex eccentricity and the ratio of anterior to posterior drag could be found. A low value of eccentricity is generally regarded as desirable for efficient streamlining (BAYLEY, 1958); velocity gradients at surface-fluid interfaces (to be discussed later) and forces of selection independent of drag minimization may well distort the predictive validity of such a result from main-stream fluid mechanics. In this context, it is interesting to note that limpets living on kelp stipes experience for the most part unidirectional flow, and might well be expected in the interests of streamlining to have an apex shifted far forward (low X). This is in fact observed in the kelp limpet *Helcion pellucida* (= *Patella pellucida*), with an apex eccentricity of 0.59 (WARBURTON, 1976). It should be mentioned that kelp limpets often possess a convex base corresponding to an excavated concavity in the kelp stipe. For those kelp limpets in the present study (*Scurria scurra* and *Notoacmea insessa*), vertical deviation of the base perimeter was less than 10% of the shell height, and was thus ignored. For a sample of three shells, apex eccentricity in *S. scurra* was not less than 0.83, while for *N. insessa* eccentricity was not less than 0.71. These values compare to an overall average (9 species, 28 shells in all) of 0.80. Those species with the lowest apex eccentricities were *Collisella digitalis*, a limpet found characteristically in the intertidal spray zone, and one of the particularly large *Nacella* shells. Neither species could reasonably be expected to experience only unidirectional flow. A further complication is the general trend towards

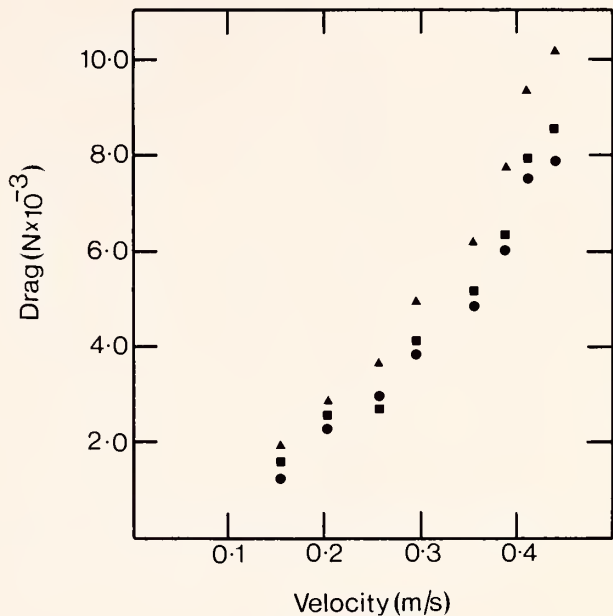


Figure 3

Variation of drag with water velocity for shell no. 25, in the anterior (●), posterior (■), and transverse (▲) orientations.

an anteriorly displaced apex among high-shore limpets with respect to their low-shore counterparts (VERMEIJ, 1978). It seems clear that apex eccentricity cannot be entirely explained as a consequence of a streamlined profile, and that other factors, such as predation (HOCKEY & BRANCH, 1983) and temperature and desiccation resistance, influence this aspect of shell form.

Transverse drag for all shells was greater than drag in a longitudinal orientation. Not surprisingly, the fineness ratio R_F is inversely correlated with the ratio of anterior and transverse drag (Figure 4). A relatively high R_F is clearly desirable in the event of unidirectional water flow, as the limpet can always preferentially orient in the current. The wave-swept intertidal zone, which can only be loosely described as a region of upward wave motion, is but vaguely reminiscent of a unidirectional current; a very high value of R_F could well be a liability under these circumstances. Given equal frontal area, the drag of bodies in free-stream flow is minimized when $R_F = 2$ (ALEXANDER, 1968). Values above two result in a higher total drag by virtue of an ever-increasing "friction drag" resulting from the forces of viscosity acting on the surface area of the body. For an object attached to a surface, the relevant value of R_F is not known, and may not be strictly comparable with the value of two given above. Nonetheless, of the 28 shells examined, the highest value of R_F was 1.68, with a mean of 1.27. Even for the stipe-dwelling limpets, minimization of drag along the anterior-posterior axis may not be the predominant factor determining the ratio of major to minor diameter.

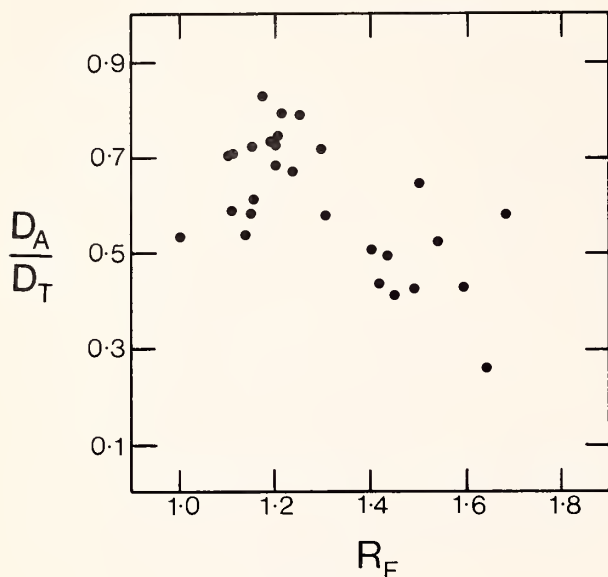


Figure 4

The ratio of anterior drag to transverse drag as a function of the fineness ratio R_F . The regression line is given by $Y = (-0.47)X + 1.21$, $r = -0.62$, $P < 0.05$.

Mean drag was found to be strongly correlated with shell length, height, and volume. The ratio of mean drag to $V^{2/3}$, where V equals shell volume, was chosen as a quantity indicative of the relative drag acting on a shell ($V^{2/3}$ being the biologically relevant reference area). This ratio increases only slightly with respect to relative shell height ($D/V^{2/3} \propto h_r^{0.32}$, $r = 0.41$, $P < 0.05$), and is not correlated with shell volume. There is admittedly considerable scatter in the data, but as a rough approximation the relative drag does not appear to increase with greater relative height or volume. Also of interest is the absence of correlation between relative drag and the ratio of the perimeter to the geometrical mean of the major and minor diameters. The latter is a dimensionless measure of the convolution of the shell's perimeter, and is thereby proportional to the amount of shell ribbing. BRANCH & MARSH (1978) reported that a slight roughening of the shell surface actually decreases the coefficient of drag (by inducing turbulent flow and thereby delaying flow separation), but that shells with pronounced radial striation experienced a higher relative drag (higher C_D). The present data, which again contain much scatter, cannot be sufficiently resolved so as to distinguish between the relative contributions of drag reduction by the induction of turbulence and the increase in drag brought on by an increase in cross-sectional area. The presence of ribbing and pronounced costae does not necessarily indicate a sheltered existence, as many wave-exposed species of limpets and other gastropods display strongly sculptured shells (VERMEIJ, 1978). Finally, the relative drag for those species generally living

in heavily wave-stressed environments (*Patella flexuosa*, *Fissurella nimbosa*, and *F. nodosa*) was significantly less than that of all other species considered (Mann-Whitney U test, $P < 0.05$). Although the sample size is small, it may not be incorrect to suggest that selection for drag-reducing features has been greater among wave-exposed species.

By virtue of viscosity, fluid velocity near a surface-fluid interface is less than the free-stream velocity. Directly at the interface there is no fluid movement. The thickness of the boundary layer is commonly defined as the distance from the surface at which fluid velocity is equal to 99% of the free-stream value. Assuming laminar flow, the boundary layer thickness δ for a flat plate parallel to flow is given by: $\delta = 5(x\mu/\rho U)^{1/2}$, where ρ and U are as defined previously, μ is the dynamic viscosity of the fluid, and x (11 cm) is the distance downstream from the leading edge of the plate (VOGEL, 1981). The assumption of laminar flow for the current situation is justified by the observation that the local Reynolds number (30,000), based upon 11 cm as the characteristic length, is less than the value generally associated with the transition to turbulent flow. Boundary layers in the present experimental arrangement, using for x the invariant distance from the leading edge of the plate to the center of the shell, ranged from 3.7 mm at $U = 0.2$ m/sec to 2.5 mm at $U = 0.45$ m/sec. These values are not insignificant when compared to the heights of particularly the smaller shells studied (Table 1). Drag of smaller shells should thus increase disproportionately with respect to larger shells as velocity is increased, because with the decrease in thickness of the boundary layer at higher velocities, a relatively greater shell area is exposed to the free-stream velocity. Figure 5 illustrates this inverse relationship between b ($C_D \propto Re^b$) and shell height. For taller limpets, C_D is roughly independent of Re ($C_D \propto Re^0$), while the very large values of b are reserved for very small shells. This finding is independently corroborated by the variation of b with shell orientation. The power b for shells in a transverse orientation was significantly less than that for shells in a longitudinal orientation (Mann-Whitney U test, $P < 0.05$). For higher absolute magnitudes of drag (transverse drag, for example, always being greater than anterior drag), the relative contribution of drag resulting from a smaller boundary layer is less. The value of b decreases correspondingly. The small values of b recorded for the larger shells may also indicate that the reported values ($b = -0.95$) of BRANCH & MARSH (1978) could be due to an error in calibration or in experimental design.

DISCUSSION

HOERNER (1965) presents coefficients of drag for protuberances within turbulent boundary layers. A round rivet head shows a $C_D = 0.32$, based on the maximum projected area (plan-form) of the head, while a highly streamlined protuberance has a C_D of 0.07. The drag coefficients for

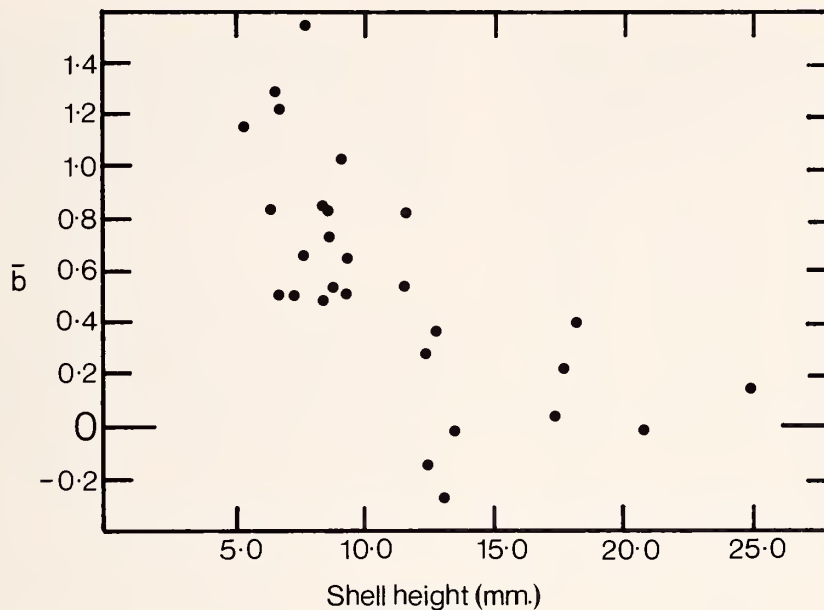


Figure 5

The variation of \bar{b} with shell height.

limpet shells (Table 2) are based on cross-sectional area, and reflect partial protrusion through a laminar boundary layer. Since in both cases the mean velocity experienced by the object is less than the free-stream velocity, drag coefficients calculated on the basis of the latter will be less than those calculated with some mean velocity. A drag coefficient could be calculated for smaller cross-sectional regions of the shell, using for U the velocity at the center of each region, and then the results summed over the entire cross-sectional area, but the significance of such a compound drag coefficient is not clear. Given the absence of a well-defined method of describing mean velocity relative to shell area, and lacking any data against which to compare drag coefficients calculated in such a manner, all drag coefficients in the present study were calculated with the free-stream velocity. It is nevertheless interesting that the values for limpet shells are generally between 0.07 and 0.32, suggesting that limpets have adopted, in comparison with a symmetrical round form, a better streamlined profile. As mentioned above, relative drag is less for those limpets living in wave-stressed environments, indicating that there may be selective pressure for the reduction of fluid-dynamic drag. There are two other forces generated by water movement that could potentially be of biological significance, namely shock pressures and acceleration forces. The former is a transient force corresponding to the establishment of flow in a temporarily stopped mass of fluid, while the latter is the force exerted on an object by the acceleration of the fluid displaced by the object (the so-called added mass). CARSTENS (1968) states

that, for continuous wave trains in shallow water, acceleration forces are likely to be negligible for bodies that are small in comparison to the wave height, and the shapes that minimize fluid-dynamic drag also minimize shock pressure, which in any event only rarely reaches extreme values, so that the concomitant drag associated with these forces is likely to be small for limpet shells (see however DENNY [1982] for description of a more complicated situation of flow). It should be noted that limpets are easily dislodged by wave surges if they have not anticipated, by means of clamping down in response to low velocity currents, a strong current flow (WARBURTON, 1976).

The hydrodynamic significance, if any, of shell sculpture remains unclear, given the absence of correlation between relative shell drag and convolution of the shell perimeter. Pronounced ribbing may of course have other roles. VERMEIJ (1973) noted the presence of increased shell sculpture among sun-exposed limpets, and JOHNSON (1975) demonstrated that shells of *Collisella digitalis* have slightly lower convective coefficients than shells of *C. scabra*, which are more ribbed and spinose. Strong shell sculpture reduces vulnerability to crushing predation in many gastropods (VERMEIJ, 1978), and in limpets has been specifically suggested as a deterrent to bird predation (GLYNN, 1965). The rough surfaces of many limpet shells may also be implicated in the reduction of the forces of shock pressure through the entrainment of air (CARSTENS, 1968), and in a redistribution of instantaneous drag forces. The expression of shell sculpture may thus be determined by a number of independent factors, and any explanation

Table 2

Drag forces in newtons ($\times 10^{-3}$) for anterior, posterior, and transverse orientations (D_A , D_P , D_T), mean drag \bar{D} , the coefficient of drag (C_D), and the mean power \bar{b} .

Shell	D_A	D_P	D_T	\bar{D}	C_D	\bar{b}
1	1.61	1.70	2.61	2.13	0.17	0.40
2	0.90	0.89	1.27	1.08	0.18	0.53
3	0.49	0.44	0.90	0.68	0.17	0.85
4	0.93	0.91	1.27	1.09	0.24	0.52
5	0.56	0.70	0.77	0.70	0.19	0.80
6	0.35	0.33	0.48	0.41	0.22	1.14
7	0.87	1.00	1.70	1.32	0.14	0.51
8	0.62	0.85	1.06	0.90	0.16	0.50
9	0.30	0.32	0.70	0.51	0.14	1.09
10	0.21	0.35	0.68	0.48	0.12	0.82
11	0.17	0.25	0.40	0.31	0.10	1.55
12	0.92	0.97	1.37	1.16	0.14	0.72
13	0.72	0.84	1.35	1.06	0.20	0.66
14	0.86	0.80	1.04	1.87	0.09	0.83
15	0.47	0.53	0.96	0.73	0.15	0.64
16	0.42	0.60	0.72	0.61	0.12	1.20
17	0.43	0.45	0.60	0.52	0.15	1.28
18	1.91	2.13	3.62	2.82	0.29	0.29
19	1.13	1.12	1.96	1.54	0.31	0.50
20	1.36	1.41	2.11	1.75	0.47	0.84
21	0.54	0.57	1.22	0.88	0.06	0.21
22	0.25	0.29	0.55	0.41	0.05	0.37
23	7.35	7.37	10.09	8.72	0.33	0.14
24	3.81	3.83	4.80	4.31	0.32	-0.01
25	3.68	3.77	8.88	6.30	0.32	-0.16
26	3.62	3.66	4.53	4.09	0.27	0.04
27	2.32	2.65	3.41	3.26	0.27	-0.03
28	2.09	2.12	2.82	2.46	0.29	-0.28

of the observed intraspecific, interspecific, and geographical variation in limpet shell sculpture that is solely concerned with fluid-dynamic drag seems at this time unwarranted.

In the present experimental design, the small gap between the limpet shell and the fixed surface (0.85 mm) precludes direct identification of measured drag forces with those likely to be encountered in the field. This small distance, however, is well within the boundary layer as calculated above, and there is no reason to suspect that the very low fluid velocities in this region will distort the validity of comparisons of drag forces on different shells. Velocities required for the dislodgement of living animals are substantially greater than those used in the present work (WARBURTON, 1976), and it is possible that drag coefficients at these velocities will differ from those reported herein. Boundary layers in the field, however ill-defined in the context of breaking waves and rock surfaces, may well be smaller than several millimeters. In this case, the variation of \bar{b} with height will be of relevance to yet smaller shells, and may only be of importance in larval settlement and survival, albeit at much lower Reynolds numbers. Intertidal boundary layers can also, under con-

ditions of turbulent flow and steady wave trains, be much larger than the shell heights considered here. The result that the relationship between C_D and Re can, in certain circumstances, vary according to the height of the object above the substrate has not been previously reported, and could represent an additional consideration in the adaptation of organisms to drag forces in the intertidal zone.

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